

A NEW SPECIES OF *MESOPTYCHIA* (LINDB.) A. EVANS FROM CALIFORNIA¹

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Abstract. A small, endemic leafy liverwort found in the coastal redwood forests of Santa Cruz and Monterey Counties of California is described as a new species of *Mesoptychia* (Lindb.) A. Evans, i.e., *Mesoptychia polymorpha* Stotler, Crand.-Stotl. & Bakalin, *sp. nov.* This new taxon is morphologically related to the suite of small-leaved species of the genus, including *M. badensis* (Gottsche ex Rabenh.) L. Söderstr. & Váňa and *M. morrisoncola* (Horik.) L. Söderstr. & Váňa, but is unique within the genus in having mature vegetative leaves and bracts that are undivided and apically rounded to emarginate, with bilobed to retuse leaves of restricted occurrence. Although this polymorphic species is parocious, perianths expand without fertilization and sporophytes are unknown.

Key words: barriers to fertilization, California endemic, *Hattoriella*, leaf polymorphism, *Leiocolea*, liverwort, *Mesoptychia*, new species

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INTRODUCTION

Until recently, *Mesoptychia* (Lindb.) A. Evans was regarded as a morphologically isolated, relict taxon, with a single species, *M. sahlbergii* (Lindb. & Arnell) A. Evans, found only in widely dispersed high arctic localities. Citing molecular evidence published by de Roo *et al.* (2007), Vilnet *et al.* (2010) and Masuzaki *et al.* (2010), Váňa *et al.* (2012) have now broadened the circumscription of *Mesoptychia* also to include all species previously assigned to *Hattoriella* (Inoue) Inoue and *Leiocolea* (Müll. Frib.) H. Buch. Although a well-developed *Calypogeia*-type marsupium sets *M. sahlbergii* apart from *Hattoriella* and *Leiocolea*, molecular analyses have consistently

resolved it nested among accessions of these taxa. In fact, despite differences in androecial and paragynoecial organizations that seemed to warrant their separation at generic, subfamilial, or even familial ranks by past authors (Evans 1903; Schuster 1969; Steere & Inoue 1975; Crandall-Stotler *et al.* 2009a, b), an intrageneric relationship among these taxa is supported by similarities in leaf and underleaf form, perianth morphology and capsule wall anatomy. The principle of priority deems that *Mesoptychia* be the generic name for this complex of taxa, as implemented by Váňa *et al.* (2012).

Among collections made by W. T. Doyle in coastal areas of Monterey and Santa Cruz Counties of California we have found a small ‘*Leiocolea*-like’ hepatic that unpublished molecular analyses suggest is an un-described species of the *Mesoptychia*/*Leiocolea* complex (J. Shaw *et al.* unpublished

¹ In recognition of his illustrious career in hepaticology, this contribution is dedicated to Professor Doctor Tamás Pócs on the occasion of his 80th birthday.

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data). Populations of this new taxon have been located in only a few sites in the summer fog belt, typically along creeks in coastal redwood forests. The small leafy plants can form fairly extensive mats or may be scattered as individuals among other bryophytes, on damp, shaded, often vertical substrates near water, frequently at seasonally inundated sites, near cascades, or either permanent or small ephemeral waterfalls. A morphological study and circumscription of this new species, populations of which have been monitored for nearly 20 years, is the focus of this contribution.

MATERIALS AND METHODS

Serial paraffin sectioning and scanning electron microscopy (SEM) were used to study perianth-bearing shoots found in two collections, while general morphological features were recorded from all collections using standard optical microscopy. Detailed specimen information for all samples studied is included in the taxonomic treatment. For serial sectioning, freshly collected plants were preserved in formalin-acetic acid-ethanol (FAA) solution, dehydrated in a graded tertiary butyl alcohol (TBA) series, and infiltrated and embedded in Paraplast Plus, following standard techniques (Jensen 1962). Serial sections were cut at 8 μm on an AO Spenser 820 rotary microtome, fixed to glass slides with Haupt's adhesive (Haupt 1930), stained with contrasting Iron Alum Safranin O (Gray & Pickle 1956) and 1% fast green FCF in 70% ethanol. Cover glasses were mounted using Histoclad mounting medium. Optical images were captured with either an Olympus SZX12 dissecting microscope equipped with an Optronics digital camera or a Leica CTR 5000 compound microscope with a Q Imaging Retiga 2000R camera. To improve depth of focus, multiple images were stacked in Helicon Focus ver. 3.79.

For SEM, shoots were fixed overnight at 4°C in a solution of 2% glutaraldehyde-2% paraformaldehyde in 0.1 M sodium cacodylate buffer, pH 7.2, and then post-fixed in 4% aqueous osmium tetroxide for 4 hrs. Following dehydration in a graded ethanol series, specimens were critical point dried in a Tousimis Samdri CPD, using CO₂ as the transition fluid, mounted on stubs with double sticky tape, and coated with 400 Å of gold-palladium in a Denton Desk II sputter coater. Specimens were viewed and digital images captured with a Quanta FEI 450 SEM.

RESULTS

Our studies confirm that the '*Leiocolea*-like' plants from California, although similar to other taxa currently recognized in *Mesoptychia*, are morphologically different from all of them and in accord with the unpublished molecular data of J. Shaw *et al.* should be recognized as a new species. Like many other species of the genus, these small, little branched plants have very oblique, almost longitudinally inserted leaves (Figs 1–3, 8), lanceolate to highly reduced underleaves (Fig. 4), cells with striolate walls and granulate oil bodies (Figs 5, 6), often dense, widely scattered rhizoids (Fig. 10), only slightly modified male bracts (Figs 9, 10) and a smooth, non-plicate perianth with a crenulate to rarely beaked mouth (Figs 1, 10, 11). The most striking attribute of this new taxon is the pronounced variation that occurs in leaf, underleaf and perianth form, both within and among populations. We have chosen the epithet *polymorpha* for the species as a descriptor of its phenotypic variability.

Mesoptychia polymorpha Stotler, Crand.-Stotl. & Bakalin, *sp. nov.* Figs 1–13

HOLOTYPE: UNITED STATES: CALIFORNIA. Santa Cruz County, Nisene Marks State Park, Aptos Creek nr George's Picnic Area, ca 165 ft alt, T11S R1E, 26 Nov. 2007, Doyle 11541 (F; ISOTYPES: G, TNS, UC, VBG1).

Plants prostrate with apices slightly ascendant, intertwined with mosses in thin mats, small and delicate, (0.6–)0.8–1.0(–1.5) mm wide and less than 6 mm long, in nature pale yellow green without secondary pigments, becoming light yellowish brown when dried, little branched, with branches only of the lateral, endogenous *Plagiochila*-type. Stems elliptical in transverse section, 140–180 μm wide by 100–125 μm high, 5 to 8 cells in broadest diameter, with the cells uniformly thin-walled, lacking trigones, isodiametric internally to short-rectangular in the epidermis, becoming smaller and quadrate in the ventral epidermis; in surface view, dorsal epidermal cells elongate, 25–35 μm wide by (40–)45–90(–150) μm long, with 1 central row always leaf-free, ventral epidermal cells 12–20 μm wide by 18–72 μm long, with rhizoid initials and

rhizoids produced centrally. Rhizoids sparse to abundant, scattered along the ventral surface of the stem, grayish-brown, smooth-walled and unbranched. Leaves obliquely inserted, succubous, not or only weakly decurrent dorsally, not decurrent ventrally, horizontal, distant to contiguous on most stems, becoming imbricate on more robust and fertile shoots, highly variable in shape, from broadly obovate to obtusate, rectangular or lingulate (elliptic), with the apices varying from obtuse to truncate, or retuse, emarginate or shallowly to deeply bilobed, with the lobes acute to obtuse and unequal in size. Leaf cells isodiametric to elongate, (27–)30–44(–46) μm wide by (30–)34–60(–65) μm long, thin-walled, with trigones absent, with the walls finely striolate; oil bodies (2)3 to 5(8) per cell, elliptical to spheroidal, gray, coarsely granulate, 3.8–5.7 μm in diameter and up to 9.5 μm long. Underleaves present or absent, highly variable in size and form, usually reduced to a uniseriate filament, (1)2 or 3 cells long, with a terminal slime papilla, sometimes with 2 cells forming a basal lamina from which arise 2(3) unequal filaments, or occasionally foliar, 4 cells wide at the base, 2 cells wide above, and 8 cells long, measuring 45–50 μm in width by 280–300 μm in length, the latter form found primarily near the base of robust branches. Gemmae absent.

Paroicous. Androecium just below and including the female bracts; male bracts gradating into female bracts in (2)3 or 4 series, equal to or larger than the vegetative leaves, inserted obliquely, becoming subtransverse dorsally, with the dorsal insertion often extending over the midline, concave and somewhat inflated at the dorsal base, ensheathing the stem, imbricate, erecto-patent, quadrate, with the margins somewhat crispate, and the apices emarginate to shallowly bilobed, with the lobes asymmetric, somewhat reflexed and apically obtuse; antheridia 1(2) per bract, small, hyaline, obovate, with the jacket cells untiered and the stalk uniseriate, 5 to 7 cells long, associated with 1 or 2 short axillary slime hairs, 2 or 3 cells long; bracteoles absent or highly reduced. Gynoecia terminal, usually with 1 subfloral innovation of the endogenous *Plagiochila*-type; bracts in 1 series just below the perianth, often with 1

axillary antheridium, transverse to subtransverse, larger than the leaves, quadrate to slightly wider than long, with the margins entire, undulate, and the apices undivided, broadly rounded and somewhat reflexed; up to 20 archegonia per gynoecium; bracteole absent or present, when present variable in form, usually small, less than 120 μm long, of 1 or 2 uniseriate filaments, 3 to 6 cells long, with 3 to 5 slime papillae, rarely large and lanceolate, 1.0 mm long by 0.4 mm wide, with a 3-celled lateral tooth; perianths developing without included sporophytes, elongated beyond the bracts, unistratose throughout, clavate to obpyriform, up to 1.4 mm long, 350–400 μm wide basally, expanding up to 900 μm wide above, smooth, contracted at the mouth, with the mouth crenulate with elongate cells, not beaked or rarely very shortly beaked. Sporophytes unknown.

ADDITIONAL SPECIMENS EXAMINED [PARATYPES]. UNITED STATES: CALIFORNIA. SANTA CRUZ COUNTY. Nisene Marks State Park, Aptos Creek nr Porter Picnic Area, ca 45 m alt, 13 Dec. 1994, *Doyle 7056* (UC); 29 Jan. 1996, *Doyle 8067* (UC); nr George's Picnic Area, ca 50 m alt, 17 Jan. 2003, *Doyle 10341* (UC); 6 March 2003, *Doyle 10341B* (UC); nr George's Picnic Area, on vertical mudstone bank, 13 July 2008, *Crandall-Stotler & Stotler 4668* (F); below bridge crossing of Aptos Creek on vertical sandstone canyon walls of creek in shade, NAD 83: 37°00'05.0"N, 121°54'22.2"W, 300 ft alt, 8 June 2013, *Shevock 42537* (CAS, F); on moist, shaded, mudstone wall above a seasonal feeder creek of Aptos Creek, 37°00'59"N, 121°54'24"W, 100 m alt, 6 Apr. 2008, *Kellman & Shevock 5858* (CAS); seep with *Adiantum* ferns over sandstone rockwall of streamlet 0.01 mile from junction with Loma Prieta Grade Track, NAD 83: 37°00'58.4"N, 121°54'20.7"W, 350 ft alt, 8 June 2013, *Shevock 42524* (CAS, F); seep over sandstone rockslab at creek, below junction of Bridge and Aptos Creeks, NAD 83: 37°01'31"N, 121°54'06"W, 350 ft alt., 13 July 2008, *Shevock, Kellman & Buck 31788A* (CAS); vertical sandstone walls along Aptos Creek near the Porter House site, NAD 83: 37°01'31.2"N, 121°54'09.8"W, 380 ft alt, 8 June 2013, *Shevock 42533* (CAS, F, MO, NY, UC). MONTEREY COUNTY. Los Padres Natl. Forest, Soda Springs Creek ca 6.3 mi S of Gorda, E side of CA Hwy 1, ca 200 m alt, R5E T24S S32, 21 March 1994, *Doyle 6135* (UC); ca 205 m alt, R5E T24S S32, 27 Apr. 1994, *Doyle 6324* (UC); S of Big Sur on CA Hwy 1, ca 260 ft alt, T20S

R2E S13, 6 May 1994, *Doyle 6448* (UC); Redwood Gulch, E side of CA Hwy 1, ca 180 m alt, R5E T24S S14, 16 May 1994, *Doyle 6458* (UC); Limekiln Creek State Park, ca 50 m alt., R4E T22S S15, 10 July 1995, *Doyle 7474* (UC); ca 60 m alt, R4E T22S S15, 25 March 1997, *Doyle 8888* (UC).

ECOLOGY. Like other species of *Mesoptychia*, *M. polymorpha* is restricted to continuously moist, deeply shaded calcareous substrates. To date, it has been found in only a few sites in the coastal redwood forests in Monterey and Santa Cruz counties of California, at elevations from 45 to 210 m on damp, vertical, consolidated mudstone rock walls of fine-grained sediments along stream channels, or on thin soil over limestone outcrops and boulders near ephemeral water falls. The plants can form fairly extensive mats that often also include *Porotrichum bigelovii* (Sull.) Kindb., *Kindbergia praelonga* (Hedw.) Ochyra, *Eucladium verticillatum* (Brid.) Bruch & Schimp. and *Pohlia longebracteata* Broth.; occasionally, a few thalli of *Cryptomitrium tenerrum* (Hook.) Austin ex Underw. and prothalli of *Adiantum aleuticum* (Rupr.) Paris are also present. In addition to *Sequoia sempervirens* (D. Don) Endl., shade trees most frequently occurring in the surrounding forest are *Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Canon & S. H. Oh, *Acer macrophyllum* Pursh, *Pseudotsuga menziesii* (Mirb.) Franco, *Umbellularia californica* (Hook. & Arn.) Nutt. and *Quercus agrifolia* Née.

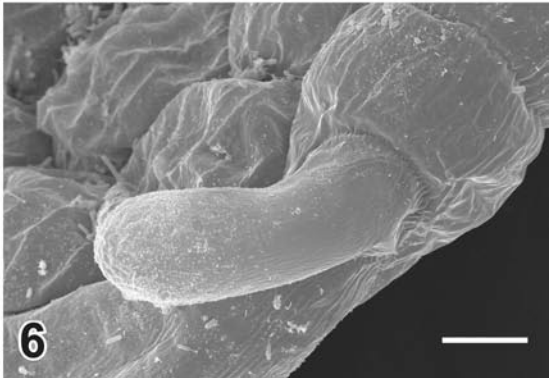
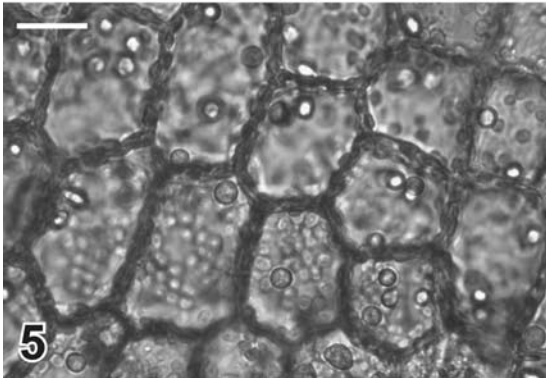
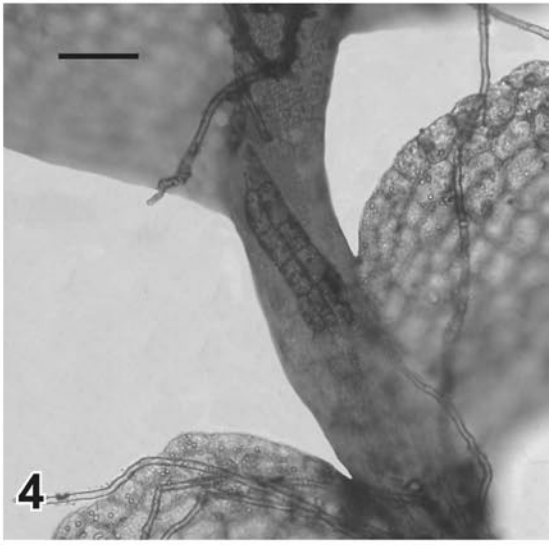
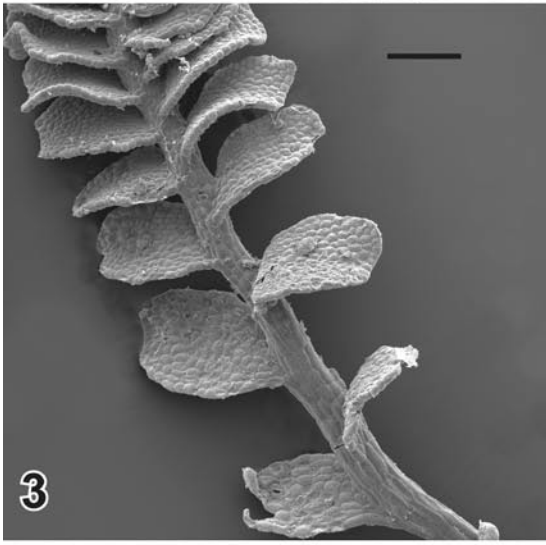
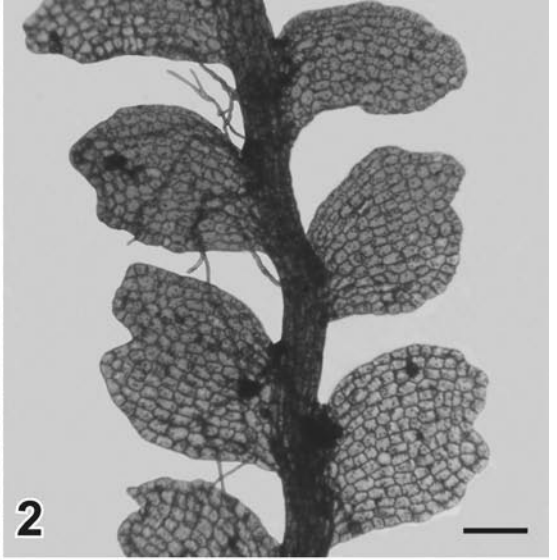
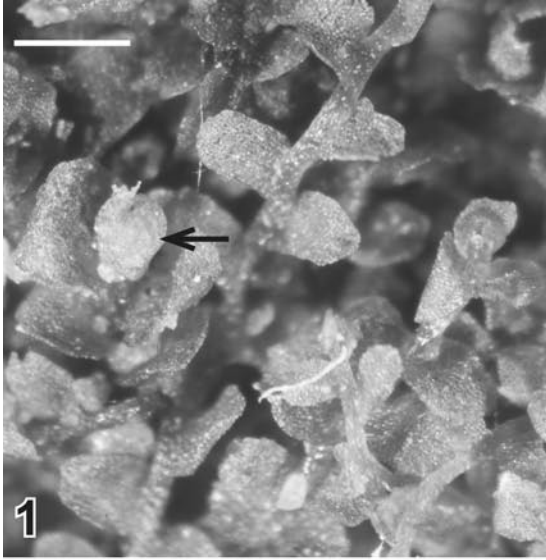
DISCUSSION

Mesoptychia polymorpha is morphologically most similar to species of the *M. badensis* (Gottsche ex Rabenh.) L. Söderstr. & Vána complex, including

species previously placed in the genus *Hattoriella* (Inoue) Inoue. In fact, its relationship to these taxa is also supported by molecular studies (J. Shaw *et al.* unpublished data). Of the species within this complex, only *M. badensis* is widely distributed in the northern hemisphere, including North America, although it has not been reported from California (Schuster 1969; Doyle & Stotler 2006). *Mesoptychia turbinata* (Raddi) L. Söderstr. & Vána is not known outside of the Mediterranean area of Europe and North Africa (Schuster 1969), while *M. chichibuensis* (Inoue) L. Söderstr. & Vána, *M. mayebarae* (S. Hatt.) L. Söderstr. & Vána [= *Hattoriella mayebarae* (S. Hatt.) Inoue], and *M. ussuriensis* (Bakalin) L. Söderstr. & Vána have rather restricted distributions in eastern Asia (Kitagawa 1966; Bakalin 2008). *Mesoptychia morrisoncola* (Horik.) L. Söderstr. & Vána [= *Hattoriella diversiloba* (S. Hatt.) Inoue] has a broader distribution in Asia, with populations known from Bhutan, southwest China, south Siberia, Taiwan and Japan (Inoue 1960; Sun & Cao 2001; Bakalin 2003).

In addition to small plant size, *M. polymorpha* shares with all of these taxa fragile, somewhat translucent shoots, leptodermous leaf cells, vestigial to small, lanceolate underleaves and smooth perianths that can be beaked, but are often simply contracted at the crenulate mouth. Gametangia are rarely produced, but when present, are paroi-cous, in contrast to the dioicous sexual condition of *M. badensis*, *M. turbinata*, *M. mayebarae* and *M. morrisoncola*. Paroi-cy is also expressed by *M. chichibuensis* and *M. ussuriensis* (Kitagawa 1966; Bakalin 2008), but both of these taxa possess asymmetrically bilobed leaves and bracts that immediately distinguish them from *M. polymorpha*, in which both leaves on the upper part of mature,

Figs 1–6. *Mesoptychia polymorpha* Stotler, Crand.-Stotl. & Bakalin, *sp. nov.* 1 – Habit of several plants growing in a mat, showing one plant with an expanded, shortly beaked perianth (at arrow), dorsal view; 2 – a single vegetative shoot, showing shortly bilobed to retuse, obovate leaves near the shoot base transitioning into oblong, entire leaves nearer the shoot apex, dorsal view; 3 – SEM of a subfloral innovation, showing small bifid leaves near the branch base and larger, entire to emarginate leaves above, dorsal view; 4 – ventral view of a shoot, showing a single, well-developed lanceolate underleaf near the shoot base; only a few vestigial ventral papillae were found elsewhere on this stem; 5 – thin-walled, median leaf cells with oil bodies and parietal plastids; 6 – SEM of the margin of a female bract, showing a marginal slime papilla and cell wall striations, dorsal view; note that although such wall markings in *Mesoptychia* have been described as a ‘striolate cuticle,’ these markings are actually formed by internal deposits in the wall, not by an external cuticle. Scale bars: 1 = 500 µm; 2 & 3 = 150 µm; 4 = 100 µm; 5 = 12 µm; 6 = 8 µm. Figures 1, 2, 4 & 5 from *Doyle 10341*; figures 3 & 6 from the holotype, *Doyle 11541*.



reproductive shoots and bracts are entire to retuse, never bilobed (Figs 1, 8–11). Although a bilobed leaf form is expressed by *M. polymorpha*, leaves of this morphology are found exclusively on small shoots or at the base of longer shoots and branches (Figs 2, 3). In the latter case, they transition into the larger, unlobed leaf form as shoot growth progresses. Interestingly, it is common to find well-developed lanceolate underleaves on those shoots or portions of shoots that bear the bilobed leaves (Fig. 4), and either small, vestigial or no underleaves on the more robust, entire-leaved shoot segments, including the terminal androecia and gynoecia. These observations suggest that in *M. polymorpha* the ‘bilobed leaf with underleaf present’ morphology is a juvenile expression that is ontogenetically supplanted by unlobed leaves and loss of underleaves, perhaps related to a change in apical cell parameters associated with shoot growth. Although underleaf reduction or absence is common in all species of the *M. badensis* complex, no other species of *Mesoptychia* ever produces unlobed leaves or bracts like those of *M. polymorpha*.

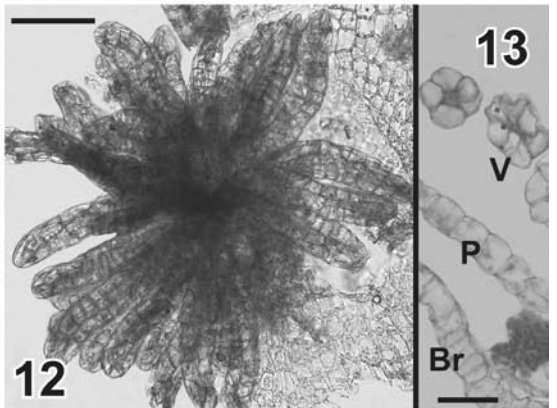
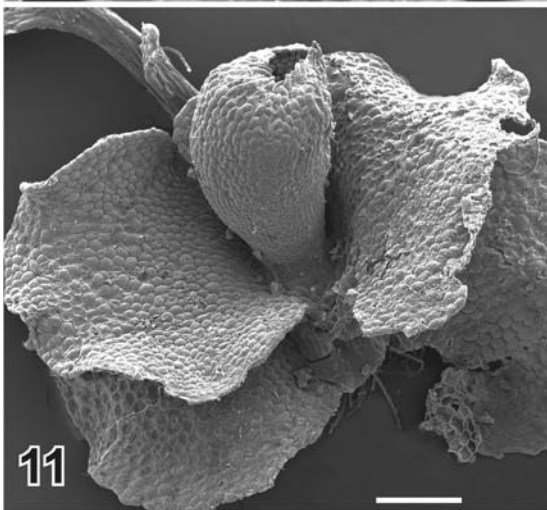
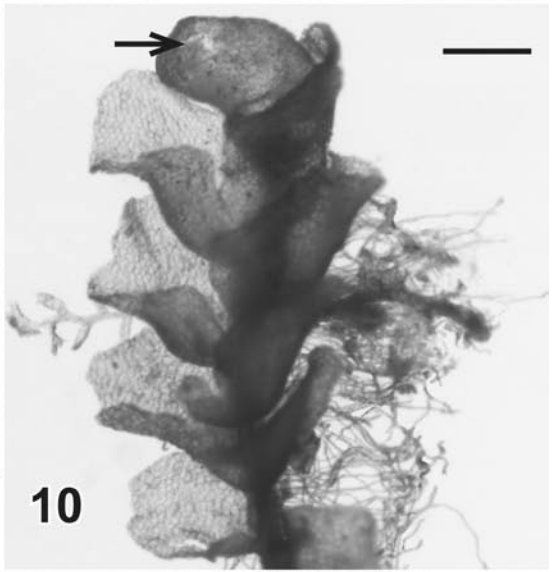
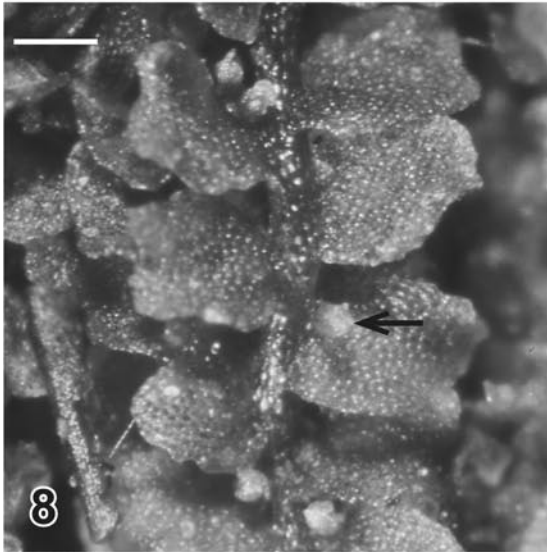
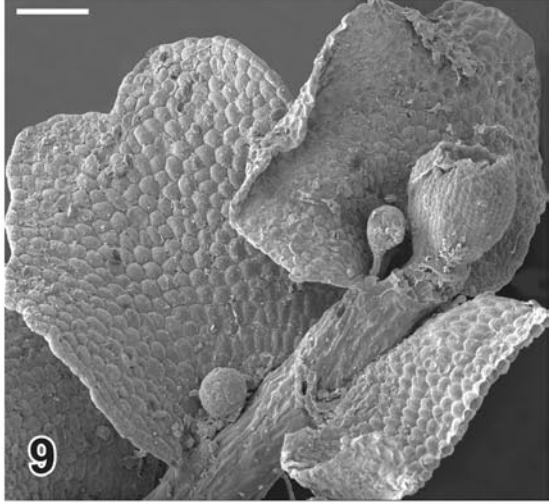
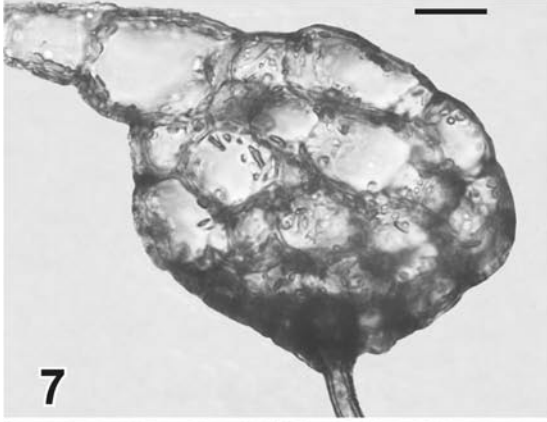
Within its restricted, sheltered habitats, *M. polymorpha* appears to reproduce and spread asexually by branching and fragmentation, perhaps with small fragments and branches dislodged and carried by stream waters during the winter rainy season. With summer drawdown, such fragments could then become established in new sites along the same waterway. In this regard, in a collection made in January 2003 (Doyle 10341) a few of the robust stems had numerous small lateral branchlets

present (Fig. 8); whether these would normally continue growth in place or become detached as small buds could not, however, be determined. Spread of fragments from one waterway to a separate waterway in the Monterey and Santa Cruz County sites would, of course, require some other type of dispersal agent.

Only vegetative plants have been found in the six sites in Monterey County, but plants bearing gametangia have been found in three sites in Nisene Marks State Park in Santa Cruz County, namely nr Porter Picnic area (Doyle 7056, 8067), nr George’s Picnic area (Doyle 10341, 10341B and 11,541) and nr the Porter House site (Shevock 42533). Surprisingly, despite repeated, extensive searches of the Aptos Creek watershed, sporophytes of *M. polymorpha* have never been found. However, collections made at the first two sites in November, December, January, and March do contain plants with antheridia and large, expanded perianths (Figs 1, 11) as well as plants with very young perianths still hidden by the bracts (Fig. 9). Plants in which the perianths have expanded typically have a single well-developed lateral *Plagi-ochila*-type innovation, which is itself terminated by a young gynoecium and hypogynous androecium. According to Paton (1999), fertilization can be irregular in paroicous species of *Leiocolea* (= *Mesoptychia*), despite the close positioning of antheridia and archegonia. However, in the absence of fertilization, perianths usually remain small and inconspicuous. An exception is seen in *M. heterocolpos* (Thed. ex Hartm.) L. Söderstr. & Váňa, in which perianths may expand to 0.8 × 1.6 mm

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Figs 7–13. *Mesoptychia polymorpha* Stotler, Crand.-Stotl. & Bakalin, *sp. nov.* 7 – Stem in transverse section; 8 – robust stem bearing numerous lateral branch buds (at arrow), dorsal view; 9 – SEM of a young sexual shoot, showing a developing perianth and subtending bracts bearing developing antheridia, dorsal view; note that one of the gynoeical bracts has been removed to expose the perianth; 10 – paroicous shoot in which the perianth has expanded without fertilization, dorsal view; note the basally inflated male bracts that transition into the single pair of bracts associated with the perianth, and the contracted, but unbeaked perianth mouth (at arrow); 11 – SEM of an expanded perianth, similar to but slightly shorter than that shown in figure 10, showing the contracted, unbeaked mouth lined with elongate cells, dorsal view; note that at this stage of development, the antheridia are no longer present; 12 – cluster of approximately 20 archegonia, dissected out of an expanded perianth; note that all of the archegonia are still closed with cover cells; 13 – serial transverse section of a young gynoecium, showing an archegonial venter (v) that is only slightly larger than the archegonial neck positioned next to it; note that the dark cluster located between the bract (Br) and the perianth (P) is part of an antheridium. Scale bars: 7 & 13 = 30 µm; 8 = 350 µm; 9 = 120 µm; 10 = 300 µm; 11 = 250 µm; 12 = 70 µm. Figures 7, 10, 11 & 13 from the holotype, Doyle 11541; figures 8 & 9 from Doyle 10341; figure 12 from Doyle 8067.



without fertilization (data from Paton 1999: 226). We have observed perianths that are up to 1.4 mm long in populations of *M. polymorpha* at Nisene Marks State Park, without evidence of fertilization (Figs 10, 11). Dissection of such perianths showed a large cluster of up to 20 archegonia, the necks of which were still closed with cover cells (Fig. 12). The venter regions of the archegonia were little enlarged, as also verified in sectioned samples (Fig. 13). Of the several perianths examined, one found in *Doyle 7056* (collected in late December 1994) appeared to enclose a very small calyptra, which is suggestive of fertilization. However, serial sections made of another perianth taken from *Doyle 10341* that looked like it had a calyptra inside was found to contain only a few unfertilized archegonia and cellular debris. It should also be noted that the perianth in *Doyle 7056* was similar in dimensions to the one illustrated in figure 10, which was verified to enclose only unfertilized archegonia. In fact, it is possible that even with fertilization, embryo development might be aborted.

Indeed, whether *M. polymorpha* has the ability to produce viable sporophytes remains equivocal. At present, we can simply speculate as to why fertilization and sporophyte formation are lacking. One explanation might be that antheridial maturation is not synchronized with archegonial development, as suggested in Figure 9. The antheridia that reside closest to the young perianth and its included archegonia mature only after perianth elongation has begun. This mechanism would enhance cross-fertilization, but would make self-fertilization rare. Since shoots with gametangia are few and very widely scattered in the population, the potential for cross-fertilization is also low. The fact that perianths elongate substantially without fertilization, perhaps prior to archegonial maturation, also generates an obstacle to fertilization. In this regard, we note that archegonia dissected out of elongated perianths are still closed (Fig. 12); i.e., they are not receptive, or ready, for fertilization. Or, there may be some type of genetic abnormality that interferes with normal gametangial development and gametogenesis. Regardless of cause, an absence of

sporophytes does help explain the restricted range of this newly named California endemic.

ACKNOWLEDGEMENTS. We thank Keneth Kellman and James R. Shevock (CAS) for taking BC-S and RES to the type locality at Nisene Marks State Park and for sharing their specimens and field observations with us to make this study more complete. We also thank Dale Vitt (SIU) and James R. Shevock (CAS) for providing identifications of the associated mosses. Financial support provided by NSF grant EF-0531750 (Assembling the Liverwort Tree of Life) to BC-S & RES is also gratefully acknowledged. The work of VB was partially supported by the Russian Foundation for Basic Researches (12-04-91150, 13-04-00775).

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Received 30 April 2013